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Studies on Costa Rican Odonata.

V. The Waterfall-Dwellers: *Thaumatoneura* imagos and possible male dimorphism.

By PHILIP P. CALVERT, PH.D., University of Pennsylvania, Philadelphia, Pa.

(Plate XIV.)

HISTORY.

In June, 1897, the late Robert McLachlan, of London, described a new and remarkable dragonfly under the name *Thaumatoneura inopinata*. He introduced his description with these words: "At the recent sale of the collections formed by the late Mr. Reginald Cholmondeley, of Condovery Hall, Shrewsbury, I obtained the few *Odonata*, solely on account of a large Calopterygine, which was evidently something unknown, but the remarkable nature of which I did not fully realize until after it came into my possession. The former owner of the collection valued insects and other natural productions, solely for their beauty or forms, and cared little for names, and nothing for localities, so I am unable to say whence this specimen came; but as the pin (or rather skewer!) was similar to those used for some other insects in the same collection which were Chinese or Japanese in origin, I hazard a conjecture that it may belong to the same region." In August,

1900, however, he was able to state that this insect belonged to the New World, as M. Martin possessed a specimen from Chiriqui, in Panama.

About 1903 Mr. C. F. Underwood collected at Carrillo, Costa Rica, six males of *Thaumatoneura* and sent them to London, where they were acquired by Dr. F. D. Godman, and sent to me for study. Four of the six were the *inopinata* of McLachlan with the middle of each wing crossed by a broad, dark brown band. The other two had the wings uncolored, wherefore they received the name *Thaumatoneura pellucida* (Calvert, 1904).

On June 23, 1909, the first day of our first stay at Juan Viñas, Costa Rica, our lepidopterological friends, Messrs. William Schaus and J. Barnes, gave us some Odonata which they had taken there for us, including some males of both *inopinata* and *pellucida* and two female *Thaumatoneuræ*, so different from the males that it was impossible to determine to which of the two species they should be referred; they had the *tips* of all the wings dark brown. Thereafter, *Thaumatoneura* became for us one of the principal attractions of Juan Viñas, that delightful spot which, as readers of the NEWS are already aware, furnished us with the remarkable larvae of *Cora*, of *Mecistogaster modestus*, and of other species still to be described.

HABITATS AND HABITS.

Of all the localities in Costa Rica which we visited, Juan Viñas was the only one where we ever saw *Thaumatoneura*. We were not at Carrillo, but in many respects the Odonate fauna of this place, judging from Mr. Underwood's collection recorded in the *Biologia Centrali-Americana*, is very similar to that of Juan Viñas. The former is on the northern, the latter on the southeastern slope of the volcano Irazú and their respective altitudes are 300 and 1040 metres (980 and 3400 feet). *Thaumatoneura* must surely live in still other places in Costa Rica.

In our experience *Thaumatoneura*, as adult or as larva, was never more than a few yards distant from a waterfall and was most abundant within its spray. The sides of the canyon

of the Rio Reventazon at Juan Viñas descend steeply from 1200 to 760 metres (4000 to 2500 feet) at the river, and down the canyon side tumble many small streams and rivulets, often in cascades and in falls of different heights. Where there is slant enough the wet rocks nearby are draped with mosses, maiden hair ferns, begonias, dwarf Selaginellas, Tradescantias, a *Streptocarpus*-like plant, etc., or in quieter more sheltered places are Mclastomes (*Miconia*), *Commelina*, etc. Only at three such falls did we ever observe *Thaumatoneura*, two of them at altitudes of about 3300 feet, the third at about 2500 feet. They were most abundant on the whole at one of the former two falls, one whose perpendicular height was the greatest of the three, perhaps 200-300 feet. We were puzzled why these insects should not be found also at other streams under generally similar conditions. An explanation of their absence from one of these streams, the little Rio Naranjo, is suggested in our diary: "At the Naranjo I saw a number of lizards from two inches to a foot in length and these possibly keep down the number of insects. At our two waterfalls [*i. e.* where we frequently found *Thaumatoneura*] we have seen no lizards."

We observed the imagos of *Thaumatoneura* in June (23-28), July 21 to August 3, September 28 and 29, when there was an evident decrease in their numbers; October 1 and December 2, 1909. In February (14-18), and March (21), 1910, none could be found, but they were again visible in April. In June, 1909, the males of *pellucida* appeared to be less numerous than those of *inopinata*. All the males of *Thaumatoneura* observed in July were pruinose, but two teneral females were taken on August 1.

"Males, at least, often remain on the same spot for a long time without moving—I should say for half an hour or longer. Females seem less persistent, but one I timed was ten minutes on the same bit of twig. Except in pairing males, the wings of both sexes, when at rest, are held in the vertical position, folded together but every now and then an individual will open and then close its wings once or several times in succession." "Standing at the bottom of the waterfall and looking up

through the spray and over the vegetation which carpets the almost perpendicular rocks, I could see the *Thaumatoneuras*—two species (*inopinata* and *pellucida*)—fluttering through the spray, chasing each other or alighting upon the rocks and plants. So heedless of the spray are they that it gathers in little drops on the wings or hangs suspended from the hind end of the body." (June 24, 1909).

"At the farther waterfall was one male each of *T. inopinata* and *T. pellucida*. I stayed here fully an hour during which there were periods of bright sunshine, but no more *Thaumatoneuras* came, and the two mentioned remained for long periods almost motionless on twigs until I caught them." (December 2, 1909).

Owing to the habit of *Thaumatoneura* of spending most of the time over vertical wet rocks, the capture of them was often only possible by climbing up on the rocks themselves, or by hanging with one hand to some long, dangling, nearby root or vine and with the other sweeping the net.

Pairing of *T. inopinata* was observed twice on June 24 and once on June 27; of *T. pellucida* once on July 30 and again on October 1. Notes made at the time on the behavior of *inopinata* are to the following effect: The male seeks and flies after the female and seizes her by her prothorax, his superior appendages being deeply inserted behind her prothorax and between it and the mesothorax, while his inferior appendages are applied against the dorsal surface of her prothorax (this from a pair which I caught and held in my fingers). After seizing the female, the male probably applies the ventral surface of his ninth abdominal segment to the ventral surface of his second abdominal segment to charge the vesicle of the latter with sperm; of this I am not entirely sure as I think I saw it but once and the operation itself occupies very little time. Male and female then assume the usual position of the Odonata in pairing. Different pairs of *inopinata* require different lengths of time to effect the attachment of the female to the male, one pair having made four or five attempts before this was accomplished, another pair effecting it at once. In one case on June 24, 1909, where I did not see the actual begin-

ning of mating, it was 3 P. M.; in the other case it began at 3.45 P. M. In both cases the male held his wings horizontal and expanded, the female had hers vertical and folded together. At the end of ten minutes the male released his hold of the female and at the same instant folded his wings together into the vertical position. The female, losing her attachment by her abdomen to the male, assumed in both cases a position about half an inch below the male resting on the same twig or rock on which he was. So the two remained for about four minutes. In the first case male and female then flew away at about the same instant, but not together, she to begin egg-laying. In the second case the female flew six inches or so away and began egg-laying while the male remained for at least ten minutes on the same spot (projecting rock) on which the pairing had occurred. In the case of June 27th, after pairing the male flew away leaving the female resting on the leaf which both had occupied.

No *pellucida* were observed pairing in June and the males of this species were less numerous than those of *inopinata*. On July 30, 1909, after some hours' watching, I saw a male *pellucida* and a female fly to a dead branch on the bank or side of the railroad cutting just west of the farther waterfall and about twenty feet above the tracks. There was no doubt that they were pairing, so it was highly desirable to capture them both. The steep bank was composed of reddish soil, loose stones and soft rock, and was wet from the rains. I climbed up as far as the steepness permitted, but the distance was still too great for the length of my net stick. After two attempts to lengthen it with branches, which chanced to be lying there, but which broke under the weight of the net, the umbrella was utilized for this purpose. Again I climbed the bank, but the soft earth gave way and collector, net and umbrella slid swiftly and separately to the railroad tracks. A second attempt had the same result. A third, made more cautiously, was so successful that the net was thrown over the accommodating pair which had lingered for at least ten minutes on the same branch and by gently dragging the net down over the bank I at last got the insects safe into my hands. Then it was that I realized for the

first time that this female was so like the females which we had seen and taken pairing with *inopinata* males that a minute comparison would be necessary to determine whether there was any difference between them or not. We saw no other pairs of *pellucida* until October 1, 1909, when one was seen and obtained at the same waterfall.

What we presumed to be egg-laying was watched in three or four instances on June 24. The female made the usual abdominal movements seen in the Zygoptera generally, that is those adapted for inserting the eggs into plant substances. Some of these movements were, however, over hard rock and it seems unlikely that any eggs were placed on it. At other times the movements were made against moss and roots. At times the female had her abdomen buried to half its length in the mass of wet moss. Pieces of roots and of moss in which the oviposition had apparently been made were carried to our room at Cartago and kept in water for months but we never obtained any larvae from them. The ovipositing female is not accompanied or followed by the male. Indeed once, on June 24, a female flew close to a resting male without attracting any response from him.

THE FEMALE.

We have three females of *Thaumatoneura* taken while pairing; one is that taken with *inopinata* male on June 27, 1909, the other two taken with *pellucida* males on July 30 and October 1 respectively. Nine other females were taken singly. All twelve females are compared in the accompanying table with respect to all the differences which I have been able to detect between the female of June 27 (No. 9) on the one hand, and those of July 30 (No. 11) and of October 1 (No. 12) on the other. It will be seen that these differences are very slight and that the positions of Nos. 9, 11 and 12 in the whole series are such as to render it unlikely that females of *inopinata* can be distinguished from those of *pellucida* by any of these features.

MALE DIMORPHISM.

This apparent lack of external characters separating the females pairing with *pellucida* males from that pairing with *in-*

COMPARISON OF THAUMATONEURA FEMALES ARRANGED IN ORDER ACCORDING TO THE RATIO $\frac{b}{a}$

	1 June 28	2 July 21	3 Aug. 1	4 Apr. 30	5 June 23	6 June 26	7 Aug. 1	8 May	9 June 27	10 June 28	11 July 30	12 Oct. 1
Length of left hind wing in mm. (<i>a</i>).....	45	48.5	49.5	49	49	49	49	50.5	46	47	49.5	48
Width of left hind wing at origin of M ₂ , measured at right angles to costa, in mm. (<i>b</i>)..	10.5	11.5	12	12	12	12	12	12.5	11.5	12	13	13
Value of ratio $\frac{b}{a}$233	.237	.242	.245	.245	.245	.245	.247	.25	.255	.263	.27
Width of left hind wing at proximal edge of brown spot at tip, measured parallel to width <i>b</i> , in mm. (<i>c</i>).....	10.	10.5	10.5	10.	10.5	11.	10.5	11.5	9.5	10.5	11.	11.
Distance from tip of left hind wing to proximal edge of brown spot measured at right angles to <i>b</i> and <i>c</i> , in mm.....	9.	10.	8.5	8	9	10	9.5	10.5	8.	9.5	8.5	9
Point of beginning of two rows of cells between M ₂ and R ₃ with reference to the proximal edge of the brown spot at tip (front wings only)	5 cells distal	distal	3 (R) 5 (L)	1 (R) 2 (L)	at (R) distal (L)	at	at	at (R) 1 cell proximal (L)	at	at	4 cells proximal	3 (R) 5 (L)
Formulae showing how the increase in density of reticulation between M ₄ and Cu ₁ begins (front wings only).....	2, 3, 3, 3, 3, 3, 3, 3, 2, 2, 3, 3, 3, 3, 3, 3, 4... (L)	2, 3, 3, 3, 3, 3, 2, 3, 3, 3, 3, 4... (L)	2, 3, 3, 3, 3, 3, 2, 2, 2, 3, 3, 3, 3, 4... (L)	2, 3, 3, 3, 3, 3, 4... (R)	2, 3, 3, 3, 3, 2, 3, 4, (R, L)	2, 2, 3, 3, 4... (R)	2, 3, 3, 3, 4... (R)	2, 3, 3, 3, 2, 2, 3, 3, 3, 3, 3, 3, 4... (L)	3, 3, 3, 3, 3, 3, 3, 3, 3, 3, 4... (L)	2, 3, 3, 3, 3, 3, 3, 4, (R, L)	2, 3, 3, 3, 3, 2, 2, 3, 3, 3, 3, 4... (L)	2, 2, 3, 3, 1... (R)
Length of the abdomen (including appendages) in mm.....	50	50	51.5	54	55	54	52	53	51	53	54	53

* Taken pairing with *inopinata* ♂. † Taken pairing with *pellucida* males

The year of No. 4 is 1910, of all others 1909.

opinata male suggests the query as to whether we are dealing with two or one species here. A number of species of Odonata are known (not to mention other groups) in which there is one form of male and two forms of females within the same species. Such are members of the genera *Ischnura*, *Anomalagrion*, *Ceratura*, *Agriocnemis* and *Neurothemis*, *Erythrodiplax umbrata* and *funerea*. While some of these so-called dimorphic females are explicable as due to differences in age, others can not be interpreted in that way. Can *Thaumatoneura* present an inverse case in which there are two forms of males and but one form of female in the same species? This leads us to consider the differences between the *pellucida* and *inopinata* males.

When I originally described *pellucida* male, I could find only two differences between it and *inopinata* male. One of these was the absence of any coloring on the wing, the other the presence of "a transverse pale citron band on nasus and on frons connecting the yellow genal spots," this band being absent in *inopinata* male. The pale citron of dried specimens, I now know, is pale blue in life. This diversity in the coloring of frons and nasus holds true for the majority of the present examples, but of the fourteen males of *inopinata* two have the pale band very well marked and three others have indications of some pale color on these parts. All fourteen *pellucida* males have the pale band. The *inopinata* males are slightly larger, average length of the abdomen 58.7, range 55-61 mm.; hind wing, average 47.6, range 45-49 mm. (14 specimens). *Pellucida*: Abdomen, average 57.25, range 52-61; hind wing, average 46.85, range 44.5-49.5 mm. (14 specimens). I have not been successful in finding any other differences in the imagos. There is no reason to think that the two forms represent age differences because no transitional individuals (so far as the presence or absence of the coloring of the wings is concerned) have been found. We have seen both forms emerge from the larval exuviae at metamorphosis, and both forms become equally pruinose on the body although so markedly different in wing coloring.

The seasonal distribution of our males is as follows: *In-*

opinata, June 23, 6 males; June 24, 2 males; June 26, 1 male; June 27, 1 male; July 21, 1 male; July 27, 1 male; December 2, 1 male; May 2, 1 male. *Pellucida*: June 23, 1 male; June 24, 2 males; June 26, 1 male; June 27, 1 male; July 22, 1 male; July 27, 1 male; July 30, 1 male; August 3, 1 male; September 28, 2 males; October 1, 1 male; December 2, 1 male; May 1, 1 male. This list gives the actualities, not the possibilities, of capture; on many occasions the insects were not molested as we wished to observe their habits and behavior. This list does show that both forms occur at the same times and, we may add, at the same waterfalls.

Among our exuviae of *Thaumatoneura* we have one from which we saw *inopinata* male emerge, another from which *pellucida* male emerged. A minute comparison of these two exuviae has failed to furnish any differences other than those due to injuries sustained by the larvae previous to transformation.

A definitive answer to the question raised on page 344 as to the relationships between the two male forms of *Thaumatoneura* to each other and to the apparently single form of female, can only be obtained from breeding experiments. As far as present evidence goes, I am inclined toward the dimorphic male hypothesis. If it prove to be true, *Thaumatoneura* would furnish a case more or less parallel to those described by Westwood (1839) for certain Staphylinidae, Leuthner (1885) for Lucanidae, and Skinner (1913) for *Lycaena pseudargiolus*.

ADDITIONAL DESCRIPTIVE NOTES.

Some additional notes on our Juan Viñas material of *Thaumatoneura* are added.

Description of the Colors of T. pellucida male, taken Dec. 2, 1909.

Description made immediately after death. Eyes dark brown, almost black. Each gena with a round yellow spot below the base of the antenna; frons between the right and left yellow spots pale blue as also is the nasus, but the fronto-nasal suture has a black line and black encroaches on each side of the nasus from below. Thoracic sutures and mid-dorsal carina lined with orange-yellow. A short occipital line, four small spots on the front prothoracic lobe and a pair of mid-dorsal spots on the middle prothoracic lobe are also orange-yellow.

The rest of the body is black, covered with pruinosity on labium, under and lateral surfaces of thorax, most of abdominal segment 1, a

large part of the dorsum of 2, a transverse basal ring on 3-7, sides of 8, much of 9 and 10, especially on the dorsum.

Legs yellowish, articulations and tarsi blackish.

The colors immediately after death of T. inopinata male, also taken December 2, 1909, agreed with those noted above for *pellucida*, including the pale colors of frons and nasus, but there was very little pruinosity except on the ventral surface of the thorax and on the posterior abdominal segments. The dark band on the wings varies somewhat in width; its proximal edge is at the nodus, its distal edge at the costa is from 16 to 20 mm. distad on the front wings, from 21 to 25 mm. distad on the hind pair. The male of May 1, however, has the proximal edge of this band 6 mm. beyond the nodus and the distal edge at 21 and 26 mm. from the nodus on front and hind wings respectively; the costal and radial spaces between nodus and the proximal edge of the band are more or less brown.

The colors of the body of Thaumatonевра females (dry, I have no notes on living colors) are as in *inopinata* males. In none of them is a distinct pale band on frons and nasus present, such as can be seen plainly on the dried *pellucida* males; Nos. 2, 5, 6, 8, 10, 11 and 12, of the table on page 343, show traces of pale color on these parts. The markings at the tips of the wings are shown in Pl. XIV, Figs. 2, 4, and the dimensions of this brown area are given in the table just quoted. Dorsum of abdominal segment 10 with a median longitudinal carina; hind margin a little excised; appendages subequal to 10 in length, straight or nearly so, a little compressed, tapering to an acute apex, black. Ovipositor proper (gonapophyses of 8 + median gonapophyses of 9) reaching caudad not as far as the level of the hind end of 10, each lateral half having ten to twelve obliquely transverse ridges on its external (ectal) surface before the apex. Genital valves (lateral gonapophyses of 9) reaching caudad beyond the level of the hind end of 10, ventral edge of each in its caudal half hairy and denticulated, hind end emarginated, valvular process attached at the deepest point of the concavity and directed caudad and ventrad.

The variation in the number of antenodals is as follows, the numbers giving percentages of wings:

	14 <i>inopinata</i> ♂	14 <i>pellucida</i> ♂	12 <i>Th.</i> ♀
Front wings			
with 3	67.87	71.4	70.83
with 3 and rudimentary 4th	3.57	3.57	
with 4	28.57	25.0	25.0
with 2			4.16
Hind wings			
with 3	75.	71.4	62.5
with 3 and rudimentary 4th	3.57	7.1	
with 4	21.42	17.85	37.5
with 5		3.57	

In all cases the "rudimentary 4th" antenodal is a small stump projecting from the anterior side of the subcosta toward, but not reaching, the costa.

The relationships of *Thaumatoneura* have been discussed by McLachlan (1897), Needham (1903), Foerster (1909), and the writer (1902, 1913).

The larva of *Thaumatoneura* will be described in the next number of these studies.

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EXPLANATION OF PLATE XIV.

Figs. 1 and 2. Male *Thaumatoneura inopinata* and female taken pairing at Juan Viñas, Costa Rica, June 27, 1909. x $\frac{3}{4}$.

Figs. 3 and 4. Male *Th. pellucida* and female taken pairing at the same place, October 1, 1909. x $\frac{3}{4}$.

Fig. 5. Right hind wing of *Th. pellucida* ♂, shown in Fig. 3. x 2 1-6. All five figures from photographs by Mr. H. A. Walters.

The Larva of *Papilio homerus* (Lepid., Rhop.).

By E. M. SWAINSON and HENRY SKINNER, M.D.

(Plate XVI, fig. 2.)

Papilio homerus, the largest American butterfly, one of the largest of the *Papilio* family, is said to be found only in the Island of Jamaica, West Indies.

The larva is very curious and differs from most of the caterpillars of the Papilionids in not having the two fleshy retractile tentacles upon the back of segment next the head. The color is green and brown; across the "neck" is a band of white, in shape something like a half moon, and on this band are spots of blue; in front of this is a band of brown with a spot at each end, in the centre of which is a line of pale blue. These spots look very like eyes when the larva is at rest. The caterpillar is about two and a half inches long. It generally rests on top of the leaf and is about the same color of green; this may account for its not being easily found as the tree is a lofty one. Five or six caterpillars will lie all together near the leaf stalk, and the eye-like spots on their heads give them the appearance of being on the watch for something.

One of us has published some notes on the occurrence of this species at Bath, Jamaica, in Volume I of the Journal of the